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THE CLASSIFICATION OF THE LEPIDOPTERA.

BY VERNON L. KELLOGG.

The new provisional classification of the Lepidoptera by Professor J. H. Comstock,[1] based on characters drawn from the wing-structure, presents as its most radical departure from earlier arrangements, the erection within the order of two suborders. One of these groups, the Jugatæ, is thus defined by Professor Comstock: "This suborder includes those moths in which the two wings of each side are united by a membranous lobe, the jugum, borne at the base of the inner margin of the fore wings, and in which the anal area of the hind wings is reduced while the radial is not. The most available recognition character is the similarity in venation of the two pairs of wings; radius being five-branched in the hind wings as well as in the fore wings." This suborder comprises but two families, the Hepialidæ and the Micropterygidæ, each family containing but one genus, *Hepialus* and *Micropteryx* respectively.

The suborder Frenatæ is characterized as follows: "This suborder includes those moths and butterflies in which the two wings of each side are united by a frenulum, borne at the base of the costal margin of the hind wings, or by a substitute for a frenulum, a large humeral area of the hind wings; and in which radius of the hind wings is reduced to an unbranched condition, while in the more generalized forms the anal area is not reduced. The most available recognition character is the dissimilarity in venation of the two pairs of wings, due to the unbranched condition of radius of the hind wings, while this vein in the fore wings separates into several branches." The Frenatæ includes all the families of Lepidoptera except the Hepialidæ and the Micropterygidæ.

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[1] Comstock, John Henry. Evolution and Taxonomy: An Essay on the application of the Theory of Natural Selection in the Classification of Animals and Plants, illustrated by a study of the evolution of the wings of insects and by a contribution to the Classification of the Lepidoptera, pp. 37–113, with 33 figs. and 3 plates, in the Wilder Quarter-Century Book, 1893, Ithaca, N. Y.

Properly to estimate the value of these subordinal characters it may be necessary for systematists to acquaint themselves with the position of Professor Comstock regarding systematic work. His point of view may differ from that of some. The essential feature of it is the insistence upon the constant recognition of the theory of descent in systematic work, no matter how circumscribed the group which is being studied. " The description of a species, genus, family or order will be considered incomplete," says Professor Comstock, "until its phylogeny has been determined so far as is possible with the data at hand."

The purpose of this paper, which is merely to add a few notes of observations which seem to be confirmatory of the most conspicuous feature of this new classification of the Lepidoptera, makes it impracticable to refer at all adequately to the method proposed by Professor Comstock for phylogenetic studies, but it is necessary to call attention here to the following paragraph from the essay referred to.

"In attempting to work out the phylogeny of a group of organisms, there will arise, I believe, the necessity of distinguishing between two kinds of characters: first, characters indicating differences in kind of specialization; and second, characters indicating differences in degree of specialization of the same kind. The former will indicate dichotomous divisions of lines of descent; the latter will merely indicate degrees of divergence from a primitive type. Thus, to draw an illustration from the following pages, it is shown that there are two distinct ways of uniting the two wings of each side in the Lepidoptera; they may be united by a frenulum, or they may be united by a jugum. These are differences in kind of specialization, and indicate two distinct lines of descent or a dichotomous division of the order. Among those Lepidoptera in which the wings are united by a frenulum, great differences occur in the degree to which this organ or a substitute for it is developed; such differences may merely indicate the degree of divergence from a primitive type and may need to be correlated with other characters to indicate dichotomous divisions."

In a study of the scales of the Lepidoptera (the results of which have been elsewhere recorded[2]), a careful examination of the wing-membranes of *Micropteryx* revealed on them, in addition to the numerous specialized scales arranged in regular rows or tiers over the membrane, a covering of very fine hairs, differing radically from the scales in size, arrangement, and mode of attachment to the membrane. These minute hairs are present in all the species of *Micropteryx* I have examined, viz.: *unimaculella, mansuetella, clathrata, anderschella, chrysolepidella, thunbergella, sparmanella, aruncella, fastuosella, seppella, semipurpurella.* And further, are present in all species of *Hepialus* yet examined by me, viz.: *sylvinus, gracilis, humuli, argentata, haydenii, hecta, purpurascens, argenteomaculatus, mcglashani, behrensii* and its variety, *montanus.*

On the other hand, I have yet to discover these minute hairs in any one of the Frenatæ, though I have examined a large number of forms distributed widely over the group. I am convinced that the presence of this clothing of minute hairs on the wing-membranes of the Jugatæ is a subordinal character.

[3]This clothing may be more specifically described as follows: in *Micropteryx unimaculella,* the fore and hind wings on their upper and lower sides are sparsely covered with fine, curving, pointed, short hairs, not inserted in sockets or "insertion cups," as are the scales, and not easily rubbed off. These hairs average .005 millimeters in length, and are distant from each other at their bases a length approximately equal to the length of the hairs. The scales of *unimaculella* average from .1 to .15 millimeters in length.

In *Hepialus sylvinus* the wings are similarly covered with fine hairs, averaging from .02 to .03 millimeters in length. The scales of *sylvinus* are from .2 to .3 millimeters long, or about ten times the length of the fine hairs, which I shall hereafter refer to as the "fine hairs" or the "fixed hairs."

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[2] Kellogg, V. L., The Taxonomic Value of the Scales in the Lepidoptera, pp. 45–89, with 17 figs. and plates IX and X, Kansas University Quarterly, Vol. III, No. 1, July, 1894.

[3] This paragraph and two or three succeeding ones referring to wing-clothing are mostly quoted from my paper on the lepidopterous scales before referred to.

Beyond the availability of the presence of the fine hairs in in the Jugatæ and their absence in the Frenatæ, as a recognition character, the phylogenetic significance of this character seems to me of interest, and if I interpret it aright, especially interesting in the light of Professor Comstock's recognition of two main branches of the Lepidoptera. The Jugatæ, according to Professor Comstock, are the more generalized group of the two. The venation indicates this strongly; *Micropteryx* possesses the most generalized mouthparts to be found among Lepidoptera; and, lastly, the mode of tying the wings together is the same as obtains in many of the Trichoptera, a a group of neuropteroid insects offering many indications of affinity with the Lepidoptera. In addition to these indications, or, indeed demonstrations, of the generalized condition of the group Jugatæ, the clothing of the wings is essentially that of the [4]Trichoptera, only in more specialized state. On the wings of the Trichoptera there is a distinct clothing of fixed hairs, unstriated, not set in sockets, and not easily removed. In addition there is a sparse covering of specialized hairs, striated, set in sockets, easily rubbed off, very long and large compared with the much more numerous fixed hairs, and evidently the lepidopterous scale in generalized state.[5]

The wing-clothing of the Jugatæ is more specialized than that of the Trichoptera in two ways: first, by the degradation of the fine hairs, tending toward that total disappearance which is characteristic of the Frenatæ; and second, by a specialization by addition, in the case of the scales, which have, indeed, reached almost as high a degree of development as is to be found among the Heterocera. This high specialization of the scales in *Micropteryx* and *Hepialus* does not at all indicate a high rank for them among Lepidoptera, but merely is confirmative of the presumption that they are the existing tips of branches whose lower members have disappeared. Nor, indeed, is it necessary to believe that these branches have been long ones, for, as I have elsewhere shown[6], the specialization of scales can come about very rapidly.

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[4] I have described and compared the clothing of the wings of the Trichoptera and Lepidoptera, in some detail, in the paper on the taxonomic value of the scales of Lepidoptera (*loc. cit.*).

[5] The beginnings of this kind of wing-clothing are perhaps apparent in the Panorpidæ.

It seems probable that the stem-form of the Lepidoptera possessed a wing-clothing much like that now exhibited by the Trichoptera, and that the Jugatæ branched off before the covering of fine hairs had been lost, although the tendency of specialization had already become manifest. The phylogenetic position of the Jugatæ, indicated by their wing-clothing, quite corresponds with that indicated by the wing venation as shown by Professor Comstock.

Another characteristic of the Jugatæ, not so distinctly available as a recognition character, but of considerable phylogenetic significance, is presented by the structure of the thorax.

The thoracic structure of the common, wingless, racial form of the Hexapoda is probably pretty fairly shown by the living Campodeas. With the appearance of wings the musculature of the two hinder segments of the thorax was necessarily largely increased, and those segments increased in size and strength. The chitinous exoskeleton became especially firm and strong for the attachment of the muscles, and the two segments acquired a bulk and form proportional to the extra development of the musculature. In the more generalized of winged insects the two pairs of wings are subequal in size and importance, and are quite independent of each other. Correspondingly, the meso- and metathoracic segments are subequal in size and form. The Paleodictyoptera of Scudder, including all the Paleozoic insects, are credited by him with the following characters (among others): "thoracic segments subequally developed; both wings closely similar in shape and with a simple neuration." The condition of wings and thorax in many of the living generalized neuropteroid insects well illustrates this state. (See fig. 1, plate XVII.)

But the parachute-like function which these broad subequal wings subserved began to give way to a more effective aerial locomotion. A tying together of the fore and hind wings of each side to secure synchronous action, and a

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[6] See paper on scales referred to.

cephalization of the flight function, manifested by a reduction of the hind wings and a specialization of the fore wings as strongly supported firm plates for rapidly beating the air obtained. This synchronity of action by the two pairs of wings and the cephalization of the flight function, was accompanied by coincident structural changes in the segments containing the wing musculature. With the loss of independence by the two pairs of wings, and the development of their united action, the meso- and metathoraces became more and more combined until in some cases they are so nearly fused as to form a single strong box for the wing musculature. The cephalization of flight or the reduction of the hind wings and the specialization of the fore wings is accompanied by a corresponding reduction in size and importance of the metathorax, and a marked increase in size of the mesothorax.

The musculature of the legs is also, of course, contained in the thoracic segments, but where, as in the Lepidoptera, the functions of the legs are so largely reduced, so overshadowed by the flight function that the anatomy of the thorax depends almost entirely on the specialization of the wings, and where, as is also the case in the Lepidoptera, the flight function and consequent condition of the wings is of so much [7] importance in the economy of the organisms, it is evident that the testimony borne by the thoracic anatomy should be a contribution of real importance towards a comprehension of the phylogeny of the group.

As a fair example of the lepidopterous thorax in a species certainly not among the more highly specialized Lepidoptera, and admittedly not belonging to the most generalized forms, I have taken the thorax of *Actias luna*. As our interest lies in the meso- and metasegments, being the ones directly connected with the function of flight, I may omit reference to the prothorax.

The scutum of the mesothorax in *luna* (See fig. 2, plate XVII) is the largest sclerite of the dorsum, and presents a greater surface than all the rest of the dorsal sclerites of the meso- and metathorax combined. It is longer than broad, is traversed by a faint longitudinal median carina, and its posterior border presents a reëntrant angle into which the forward-projecting apex of the scutellum fits. The scutellum of the mesothorax is subtriangular in outline with rounding angles. The dorsum of the metathorax is less than one-third as long as the meso-notum. The scutum is chiefly apparent in its two lateral portions, the median portion being reduced to a narrow transverse bar; the scutellum is a small transversal sclerite with a curving anterior margin. The pleural aspect of the mesothorax is markedly greater than that of the metathorax, but the relation between them does not show such a preponderance of the mesothorax as is shown on the dorsum.

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[7] See Comstock, *loc. cit.*, p. 51.

With the specialization of the flight function indicated by a cephalization of flight, including a specialization of the fore-wings and a reduction of the hind-wings, there comes a correlative change in thoracic structure. This may be shown in *Hemaris thysbe*, one of the swift-flying sphinges, with a highly specialized venation. The mesonotum (see fig. 3, plate XVII) constitutes almost the entire dorsal aspect of the thorax, the metanotum being limited to a very narrow transverse bar, dilating laterally to more conspicuous dimensions. The scutum of the mesothorax is almost as broad as long.

Turning now to the Jugatæ, the venation of whose wings, according to Professor Comstock, is the most generalized of any among the Lepidoptera, an examination of the thorax reveals a distinctly generalized condition. In *Micropteryx unimaculella* (see fig. 4, plate XVII) the mesonotum does not exceed the metanotum in length by more than one-half the length of the latter. The general outlines of the dorsum of both segments are much alike, and the scutum and scutellum of the mesonotum resemble the equivalent sclerites of the metanotum in shape. In each segment the scutellum projects forward into an angular emargination of the hind border of the scutum. In the more specialized forms of the Lepidoptera the reduction of the metanotum is accompanied by the narrowing of the median portion of the scutum, until, in many cases, the scutum is divided, apparently, by the scutellum into two lateral pieces.

In *Hepialus humuli* (see fig. 5, plate XVII) the mesonotum is relatively larger, compared with the metanotum, than in *Micropteryx*, and there is correspondingly more of a difference of outline between the two segments, but the thorax is still distinctly a generalized one. The metanotum is about one-half as long as the mesonotum.

Nowhere else among Lepidoptera have I found so generalized a condition of the thorax, as shown by the Jugatæ, unless it be in the Tineina, where, indeed, among all Frenatæ, it would be expected. In *Tinea vestitella* the thoracic structure appears to be in a very generalized state, although the shape of the sclerites differs much from that in the Jugatæ.

An additional point of interest is adduced by a comparison of the thorax of the Jugatæ with that of the Trichoptera. A striking resemblance is apparent, as is illustrated in figures 4 and 6, one being the dorsal aspect of the thorax of *Micropteryx unimaculella*, and the other that of *Hydropsyche phalerata*. This suggests again the affinity of the Lepidoptera, through the Jugatæ, with the Trichoptera.

The patagia of the mesothorax exhibit an interesting specialization following closely the development of the flight function as indicated by the wing venation and the thoracic structure. The patagia probably function as shields or protective coverings for the insertions of the front wings, the thin lobe curving around the base of the fore-wing in a way well calculated to protect this unchitinized and vulnerable portion of the moth's body. In the swift-flying sphinges the patagia acquire a remarkable development, extending posteriorly almost to the hinder margin of the mesoscutum. In the more generalized *luna* the patagia are much less developed, and in the Jugatæ the patagia are very small and inconspicuous. The patagia are present also in the Trichoptera, and are strikingly like the equivalent processes on the Jugatæ.

A careful study of the thorax of the Lepidoptera must certainly be rewarded by suggestive results.

As to the kind of characters which these drawn from the wing-clothing and thoracic structure are, I refer to the paragraph at the beginning of this paper quoted from Professor

Comstock's essay, relating to two kinds of characters; first, characters indicating dichotomous divisions of lines of descent; second, characters indicating degrees of divergence from a primitive type. It is evident that either one of these kinds of characters may be subordinate to the other, although, at first glance, perhaps, it might seem that characters indicating differences in kind of specialization, or dichotomous divisions of descent lines, must always be superior to characters indicating differences in degree of the same kind of specialization. For example, given a dichotomous branching according to characters of the first kind, the forms along either line will be ranged according to characters of the second kind, *i. e.*, differences in degree of specialization along that line. But, in a larger view, there is, in the development of any considerable group of organism, as, for example, the class Insecta, a general tendency of specialization along some pretty distinct main line, or more or less nearly parallel lines. For example, in the Insecta may be adduced the development of the flight function accompanied, in the Lepidoptera, by a cephalization of flight indicated by the specialization of the front wings and a reduction of the hind wings and accompanied also by the specialization of the thorax in the manner pointed out in this paper. Subordinate to any general tendency, such as the development of the flight function, there will appear characters indicating dichotomous divisions of lines of descent, the methods of advance along the line of the general tendency differing in two branches of the group. An example of this is afforded by the Odonata and the Diptera; in one group the specialization of fore and hindwings has followed the same lines, in the other the specialization has resulted in the loss of the hindwings. In both instances a fine development of the flight function has been reached.

Of the kind of characters indicating in a general and large way degrees of divergence from a primitive type, these characters drawn from the wing-clothing and thoracic structures may be looked on.

EXPLANATION OF PLATE, XVII.

Fig. 1.—Meso- and metanotum of *Corydalis cornuta.*

Fig. 2.—Meso- and metanotum of *Actias luna,*

Fig. 3.—Meso- and metanotum of *Hemaris thysbe.*

Fig. 4.—Meso- and metanotum of *Micropteryx unimaculella.*

Fig. 5.—Meso- and metanotum of *Hepialus humuli.*

Fig. 6.—Meso- and metanotum of *Hydropsyche phalerata.*

In all the figures : a = scutum of mesonotum ; b = scutellum of mesonotum ; c = scutum of metanotum ; d = scutellum of metanotum ; p = patagia = paratera of mesonotum.

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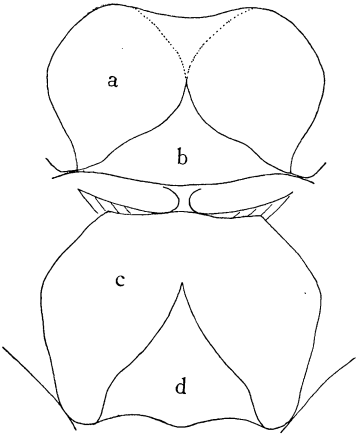
PLATE XVII.

1



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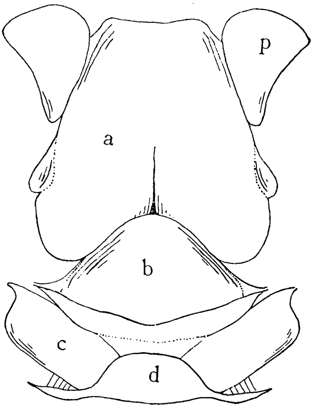

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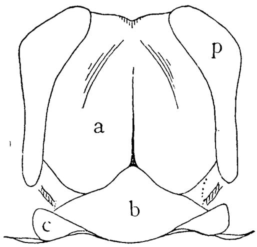

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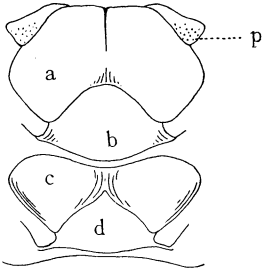

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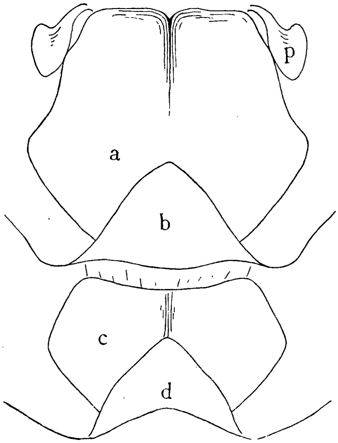

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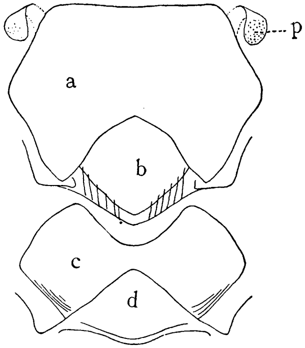

Kellogg on Lepidoptera.